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- Enhanced understanding of visual neural mechanisms underlying practice
- Practice-induced changes in neural mechanisms underlie learning
- Improvement of neurocognitive stages involved in the operation of visual attention
- Combination of series of paradigms leads to an enhancement neural responses

Enhancing Links between Visual Short Term Memory, Visual Attention and Cognitive
Control Processes Through Practice: An Electrophysiological Insight

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Abstract

The operation of attention on visible objects involves a sequence of cognitive processes. The current study firstly aimed to elucidate the effects of practice on neural mechanisms underlying attentional processes as measured with both behavioural and electrophysiological measures. Secondly, it aimed to identify any pattern in the relationship between Event-Related Potential (ERP) components which play a role in the operation of attention in vision. Twenty-seven participants took part in two recording sessions one week apart, performing an experimental paradigm which combined a match-to-sample task with a memory-guided efficient visual-search task within one trial sequence. Overall, practice decreased behavioural response times, increased accuracy, and modulated several ERP components that represent cognitive and neural processing stages. This neuromodulation through practice was also associated with an enhanced link between behavioural measures and ERP components and with an enhanced cortico-cortical interaction of functionally interconnected ERP components. Principal component analysis (PCA) of the ERP amplitude data revealed three components, having different rostro-caudal topographic representations. The first component included both the centro-parietal and parieto-occipital mismatch triggered negativity - involved in integration of visual representations of the target with current task-relevant representations stored in visual working memory - loaded with second negative posterior-bilateral (N2pb) component, involved in categorising specific pop-out target features. The second component comprised the amplitude of bilateral anterior P2 - related to detection of a specific pop-out feature - loaded with bilateral anterior N2, related to detection of conflicting features, and fronto-central mismatch triggered negativity. The third component included the parieto-occipital N1 - related to early neural responses to the stimulus array - which loaded with the second negative posterior-contralateral (N2pc) component, mediating the process of orienting and focusing covert attention on peripheral

target features. We discussed these three components as representing different neurocognitive systems modulated with practice within which the input selection process operates.

Keywords: Attention; Learning; Mismatch-triggered negativity; match-to-sample task; Visual search; N2pc; principal component analyses; Pearson–Filon statistic

1. Introduction

The operation of attention to visual stimuli typically follows a sequence of fundamental cognitive processes (Luck, 2012; Luck and Kappenman, 2012; Eckstein, 2011; Nakayama and Martini, 2011) as follows. First, a goal must be activated to guide the allocation of attention. In the case of performing a visual search task, the target's features such as colour and shape need to be stored as a *search template* in visual short term memory (VSTM) to guide attention to task-relevant objects. Second, sensitivity is increased for objects containing features specified by the *search template* so that they have priority among others for further processing. Third, there is a shift of covert spatial attention, triggered towards peripheral locations containing objects potentially sharing task-relevant features with the *search template*. Fourth, attention is adjusted and focused around the relevant object, depending on its size and the proximity of distracting objects. These last two cognitive processes are performed to facilitate the perception and storage in VSTM of task-relevant objects with the intervention of feature-based attention. The fifth step is the comparison and integration of representations of the current observed task-relevant target object and those available in VSTM as part of *search template* (Bennet, Duke, Fuggetta, 2014, Fuggetta, Bennett and Duke 2015). The current study examined the time course of Event-Related Potential (ERP) components which play a role in the processes involved in visual attention. The main purpose of the study was to enhance the understanding of which neurocognitive stages underlying the links between VSTM, visual attention and cognitive control processes can be improved through experience and practice.

The first four cognitive processes described above can overall be considered an integral part of the *input selection* construct of attention – the selection of task-relevant inputs for further processing – as defined in a theoretical framework of attention put forward by Luck

and Gold (2008). It is important to consider that the domain of input selection has been further distinguished between the *control of selection* – the process that directs attention to task-relevant items – and the *implementation of selection* – the process that enhances the processing of the relevant items and suppress the irrelevant items (Luck and Gold, 2008). The control of selection typically involves prefrontal and parietal cortices, and the implementation of selection typically occurs within the visual cortex that processes the inputs (Luck and Gold, 2008). Input selection usually depends on the executive control system to set the input selection parameters so that it will select the task-appropriate information of the to-be-attended input and suppress the to-be-ignored input.

The fifth step described above - in which representations of the cue are integrated with representations of the target in VSTM - involves an executive-control monitoring mechanism which is in place throughout the sequence of cognitive processes to perform a single rule (i.e. categorisation task). In the current study we used a novel paradigm which combines a match-to-sample task with a memory-guided efficient visual-search task (Bennet et al., 2014; Fuggetta et al., 2015). This paradigm allowed us to assess a wider range of cognitive mechanisms than in traditional visual search paradigms. In performing this paradigm, behavioural responses are slowed and less accurate when a salient target stimulus embedded in a search array of distracters contains different features from with those in the *search template* (i.e. mismatch trials), making the comparison of memory representations more demanding. Adopting Luck and Gold's (2008) framework, the current paradigm can be considered an input selection task, where a single executive control rule is used to perform the categorisation task, but a failure of input selection causes this rule to be applied less efficiently (Luck and Gold, 2008).

Previous research has established that visual search can be improved through experience or practice (An et al., 2012; Clark et al., 2015; Hamame et al., 2011; Sigman and

Gilbert, 2000; Sireteanu and Rettenbach, 1995). In particular, Clark et al., (2015) investigated the neural mechanisms underlying practice-related improvement in behavioural performance on a visual search task with target pop-out arrays. Four ERP components were assessed and found to be modulated with practice. The results showed: (1) increased amplitude of the posterior N1 component suggesting enhancement of early sensory responses to an exogenous visual array (Clark et al., 2015); for review on N1, see (Hillyard et al., 1998); (2) an earlier onset and larger amplitude of the second negative posterior-contralateral (N2pc) component, indicating enhanced attentional orienting (Clark et al., 2015), and focusing of covert attention on a peripheral location (Luck et al., 1994); (3) a reduced amplitude of the sustained posterior contralateral negativity component (SPCN), reflecting lower demands of maintaining visual information in working memory and/or target discrimination process (Eimer and Kiss, 2010; Jolicoeur et al., 2008); (4) an earlier lateralised readiness potential (LRP) (Coles, 1989), related with improvements in motor-response preparation and execution (Clark et al., 2015). However, this investigation did not assess several ERP components related to feature-based attention. Neural mechanisms which support these processes may contribute to the enhanced behavioural performance in visual search tasks with practice.

Here, we primarily aimed to extend previous electrophysiological findings (An et al., 2012; Clark et al., 2015; Hamame et al., 2011) to further enhance the understanding of visual neural mechanisms underlying improvements in behavioural performance with practice. Thus the modulation of perceptual and post-perceptual cognitive processes was investigated in a total of six ERP components that are involved in the operation of attention in vision: (1) the early sensory evoked N1, which reflects early sensory responses to the entire array (Clark et al., 2015); (2) the bilateral anterior P2, which reflects automatic detection of pop-out stimuli (Luck and Hillyard, 1994a, b); (3) the N2pc component, which reflects the process of orienting and focusing covert attention on peripheral target features (Luck et al., 2006; Luck

et al., 1994); (4) the bilateral anterior N2 (or N270), observed when subjects actively search for a target that differs from the rest of the array (Luck and Hillyard, 1994a) and for stimuli containing conflicting features (i.e. mismatch trials, for a review see Folstein and Van Petten, 2008); (5) the N2-posterior-bilateral component (N2pb) which is involved in categorising stimuli (Renault et al., 1982) and is larger for colour pop-out stimuli (Luck and Hillyard, 1994a); and (6) the post-perceptual mismatch-triggered negativity (MTN) component, which has a bilateral fronto-central and temporo-posterior scalp distribution and appears in a delayed match-to-sample task when the mismatch between the target template in VSTM and the stimulus has at least two dimensions, such as shape and colour (Bennett et al., 2014; Wang et al., 2004; Wang et al., 2003; Zhang et al., 2005).

With the number of ERP components examined in this report it might be the case that they are not independent. With so many under scrutiny, it becomes difficult to know which ones represent distinct neurocognitive processes. Thus a further aim of the study was to identify any underlying structures in the relationship between ERP components that account for unique variance and represent distinct temporal/spatial contributions to the activity observed at the scalp. To explore any such relations, we submitted the amplitude of ERP data to standard principal component analyses (PCA) with rotation. PCA methodology is a well-established exploratory analysis technique that has been used with ERP data for highlighting hidden relations that explain the most variance in a dataset as a whole (Kayser and Tenke 2005; Dien, 2012).

Correlations between behavioural and electrophysiological measures will be also implemented to examine which neurocognitive processing stages measured with ERPs are the greater contributors to the predicted improvement of behavioural performance (i.e. faster and more accurate responses) with practice. Furthermore, the modulation through practice in the association between ERP components, recorded from same or different rostro-caudal regions

of the scalp, will also be assessed. This correlation analysis will further inform us about the role of cortico-cortical interactions of functionally connected regions which might account for the predicted modulation of ERP measures (i.e. earlier onset and larger amplitude of N2pc) in association with enhancement of links between VSTM, visual attention and cognitive control processes through visual-cognitive learning.

2. Method

This study was approved by the local ethical committee of the University of Leicester's Department of Neuroscience, Psychology and Behavior, in accordance with the Declaration of Helsinki. All participants gave written informed consent and received course credit for participating. Participants were fully debriefed about the purpose of the study.

2.1 Participants

An initial group of 30 (22 females, 18–26 years, Mean \pm SE 20.31 ± 0.32 years, 26 right handed) undergraduate psychology students from the University of Leicester (UK) with normal or corrected-to-normal visual acuity and colour vision were selected to participate in the study. No participants dropped out between the sessions. All participants reported no use of medication, history of chemical dependency or neurological, psychiatric/psychological disorders or closed head injuries. Participants were excluded from further analyses if their behavioural performance (mean correct response times and accuracy) or latency/amplitude of their ERP components were above/below three standard deviations from the mean of the whole group. This selection criterion led to the exclusion of three participants. Therefore, ERP data from 27 participants (20 females, 18–26 years, 20.22 ± 0.33 years, 25 right handed) were included in all analyses.

2.2 Procedure

Participants were naïve to the purpose of the investigation. All were tested individually and participated in a match-to-sample combined with visual search protocol for approximately 1 hour on each of two days, 7 days apart. Before the beginning of the experiment on the first and second session, participants completed a ~20 min long training session to familiarise themselves with the task and adjust to the requirements. Behavioural performance (response time and accuracy) and scalp-recorded EEG were measured on both sessions of the protocol.

2.3 Stimuli and task

Stimuli were programmed using Delphi (Borland) and presented on a 21" monitor (ViewSonic G810) (40 cm horizontal \times 30 cm vertical) with a refresh rate of 100 Hz and a resolution of 1024 \times 768 pixels. The monitor was located in a black viewing tunnel so that only the display was visible. The participant's head was stabilised in a head and chin rest. Viewing distance was 57 cm. The monitor continuously displayed a white 0.4° fixation spot in the centre of a grey 26° diameter circle, shown against a black background. Four 2.1° empty white circles were present 10° peripherally in the top-left, top-right, bottom-left and bottom-right quadrants. This limited visual search to the four positions. A trial consisted of the following sequence of events, shown in Fig. 1.

< Figure 1 about here >

A centrally presented 'instruction shape' (A), either a 2° white ring (50% of trials) or an X (50% of trials) was presented for 170 ms. This shape indicated the response mapping for the current trial. If a ring was presented, then participants had to press the left key of a response box if the shapes in C and E were same and press the right key if the shapes were

different. If a trial began with an X, then participants had to press the right key if the shapes in C and E were matching and press the left key if the shapes were mismatching (See Fig 1). This method guaranteed that participants were not always using the same hand for the match/mismatch response. This part was followed by a fixation period (B) for 650 ms. This was followed by a 'shape cue' (S1), either a 2° hexagon (50% of trials) or diamond (50% of trials) and either red (50% of trials) or green (50% of trials) shown for 150 ms (C). After a delay period of 600 ms (D), the target array (S2) was presented for 130 ms (E) followed by a fixation period until a response was made (F). The target was either a hexagon (50% of trials) or diamond (50% of trials) and always of the same colour as the informative shape cue (randomised from trial to trial). The shape cue and target matched on 50% of trials and mismatched on the other 50%. The target appeared within one of the four empty white circles among fifteen homogeneous distractors (2° filled circles). Visual stimuli were spaced evenly on the circumference of an imaginary 10° radius circle around the central fixation point, as shown in Fig. 1. The distractors were always of a different colour from the target and all either red or green (i.e. either 'red target, green distractors' or vice versa). Thus the pop-out search task dimensions were both colour and shape.

The participants' task was to indicate via a response box whether the target shape (S2) (E) matched or mismatched the shape cue (S1) (C). The centre of the response box was aligned with the participants' midline. The two types of response were made with the left and right index fingers. The response mapping was alternated every eight trials as indicated by the 'instruction shape' (A) (ring vs. X) (i.e. either 'left key' for match trials, 'right key' for mismatch trials or vice versa) and counterbalanced across participants. Speed and accuracy were encouraged. Reaction time (RT) and correct/incorrect response data were recorded. Participants received auditory feedback – a 200 ms low vs. high pitch 'beep' sound, for incorrect or correct responses. A 500 ms delay time elapsed between each trial sequence.

Participants were instructed to maintain central fixation and to blink only after the ‘beep’ sound following their response. In each session, participants completed 320 trials in ten blocks of 32 pseudo-randomly distributed trials from each of the experimental conditions. Participants were allowed to pause between blocks.

2.4 EEG data acquisition

Continuous EEG signals were recorded by a DC 32-channel amplifier (1-kHz sampling rate, 250 Hz high cut-off frequency; Brain Products Inc., Germany). The EEG activity was recorded from unshielded and sintered Ag–AgCl electrodes via a Waveguard elastic cap (CAP-ANTWG64; ANT, Netherlands) using a subset of the international 10–5 electrode system sites (Fp2, F3, Fz, F4, FC5, FC1, FC2, FC6, C3, Cz, C4, CP5, CP1, CP2, CP6, P3, Pz, P4, P7, PO7, PO3, PO4, PO8, P8, O1, Oz, and O2). The right-earlobe electrode served as an on-line reference. EEG waveforms were re-referenced off-line to the average of the right and left-earlobe electrodes (Luck, 2005). Two electrodes placed in a bipolar montage at approximately 1 cm from the outer canthi of both eyes served to record the horizontal electrooculogram (HEOG). The vertical electrooculogram (VEOG) and blinks were recorded and detected from one electrode positioned below the right eye and Fp2 and referenced to the right earlobe. Electrode impedance was kept below 5 k Ω .

2.5 EEG analyses

For each participant and experimental session, those trials in which the response mapping had changed from the preceding trial were excluded from analysis. This left 280 trials with repeated response mapping. A trial was included in the analyses if the response was correct and if the RT was between 150 and 2000 ms, and also within three standard deviations from the individual's mean RT. The mean (\pm SE) number of trials analysed before

ocular artefact rejection procedure was 247.7 ± 5.6 for Session 1 and 264.4 ± 5.6 for Session 2. EEGs were epoched from 200 ms prior to target search array onset to 600 ms after, giving a total epoch of 800 ms. Each EEG epoch was visually inspected off-line, and those with ocular artefacts (as indicated by HEOG activity exceeding $\pm 40 \mu\text{V}$ and VEOG activity exceeding $\pm 80 \mu\text{V}$) were excluded. The mean (\pm SE) number of trials analysed after artefact rejection was 163.3 ± 10.8 for Session 1 and 167.7 ± 10.7 for Session 2, with a mean (\pm SE) rejection rate of $34.2 \pm 4.1\%$ for Session 1 and $36.6\% \pm 3.7\%$ for Session 2. ERPs were computed for trials relative to a 200 ms pre-target array baseline. ERPs were then filtered using 0.1 Hz high-pass (12 dB/octave), 45 Hz low-pass (12 dB/octave), and 50 Hz notch filters.

Separate average ERPs were computed for lateral parieto-occipital electrodes and Parieto-Occipital (POL/R) region of interest (ROI) consisting of a group of electrodes: P3, P7, PO7, PO3 and O1 = 'Left Parieto-Occipital region' (POL); P4, P8, PO8, PO4 and O2 = 'Right Parieto-Occipital region' (POR). To isolate the magnitude of the N2pc component elicited by the target search array, at lateral occipital P3/4, P7/8, PO7/8, PO3/4, O1/2 electrodes and POL/R sites pairs, we computed difference waves by subtracting ipsilateral from contralateral electrodes relative to the target location. To eliminate any hemispheric asymmetries that were unrelated to attention, we averaged the difference waves across left- and right-hemispheres (see Luck et al., 2006).

Separate average ERPs were computed for bilateral electrodes at rostro-caudal ROIs each consisting of a group of electrodes: F3, Fz, F4, FC5, FC1, FCz, FC2 and FC6 = 'Fronto-Central region' (FC); C3, Cz, C4, CP5, CP1, CP2 and CP6 = 'Centro-Parietal region' (CP); P7, P3, Pz, P4, P8, PO7, PO3, PO4, PO8, O1, Oz and O2 = 'Parieto-Occipital region' (PO). The mismatch-triggered negativity (MTN) component is a bilateral ERP component sensitive

1 to perceptual mismatch between an initial stimulus S1 (shape cue) and a subsequently
2 presented (mismatching) stimulus S2 (target shape) and reflecting the integration process
3 between STVM representations of the two stimuli (Bennett et al., 2014; Fuggetta et al.,
4 2015). To isolate the magnitude of the MTN component and assess the onset latency of the
5 integration process, we computed difference waves by subtracting match from mismatch
6 trials. For a detailed discussion of this analytical approach previously adopted for the P3
7 component (Luck et al., 2009), see chapter 2 in Luck (2005).
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18 It is common practice in ERP studies to choose a measurement window for the mean
19 amplitude of an ERP component by visual examination of the data collapsed across
20 conditions and participants (Kappenman et al., 2016). Here, we preferred to adopt a statistical
21 criterion to define the time window to extract the mean amplitude of both N2pc and MTN
22 difference waves across the entire group of participants. Specifically, in the case of N2pc for
23 every millisecond, a one-sample *t*-test (2-tailed) with test value 0 was conducted on the
24 contralateral minus ipsilateral difference waveforms at PO7/8 electrodes collapsed across
25 sessions. The same procedure was conducted in the case of MTN on the mismatch minus
26 match trials difference waveforms collapsed across FC, CP and PO ROIs and sessions. The
27 beginning (and end) of the time window to extract the mean amplitude of these two ERP
28 components was defined as the first (and last) time point reaching a conservative $p < 0.01$ (2-
29 tailed) which was followed (or preceded) by at least 10 subsequent milliseconds reaching
30 $p < 0.01$ (2-tailed) or less, to eliminate false alarms. These criteria are similar to those of
31 previous studies examining the origin of the macaque N2pc human homologue using a
32 “neuron–anti-neuron” approach (Purcell et al., 2013) and the human N2pc (Fuggetta et al.,
33 2015).
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To test hypotheses about the true difference in onset latency of ERP components between conditions, an estimate of variability among participants is required (Miller, Patterson, and Ulrich, 1998). ERP studies are increasingly using the jackknifing procedure to obtain accurate estimates of ERP latencies (Miller et al., 1998). This method can be simplified by retrieving individual participants' latencies with a simple procedure (Smulders, 2010). Thus here, we adopted the jackknifing procedure using the computationally simple transform put forward by Smulders (2010) to retrieve estimates of the individual participants' onset latency of both N2pc and MTN components.

The majority of studies using the jackknifing of ERPs approach use a relative criterion to define the onset latency such as the time point at which the voltage reaches 50% of the maximum peak amplitude (Kappenman et al., 2016; Luck et al., 2009). This has been considered the optimal measure of onset time under many conditions (Kappenman et al., 2016; Kiesel et al., 2008; Luck et al., 2009; Miller et al., 1998). However, Smulders, Kenemans, & Kok (1996), indicated that the 50% relative criterion is invalid in case of slope differences across conditions in the LRP. Moreover, Gratton (2007) using simulated data, pointed to the same problem that if slope or the maximum values of ERP waveforms are systematically different across conditions, then determination of the latency using a 50% relative measure of maximum amplitude may be misleading. In an attempt to circumvent this issue, in the case of different LRP peak amplitudes across conditions, a criterion of at least 30% of the peak amplitude was suggested (Miller et al., 1998). Whereas if the initial proportion of the LRP differed in shape, a relatively low criterion between 10-30% was suggested to minimise the effects of noise on the grand average (Miller et al., 1998). Taking into account these recommendations, here we retrieved estimates of participants' latencies adopting as a relative criterion the point at which the N2pc and MTN difference waves reached 12.5% of the peak amplitude. See supplementary material 1 supplied as Word file

and open raw research data 1, supplied as an Excel file for further details of the procedure used to retrieve estimates of participants' ERP onset latencies.

< Supplementary material 1 about here > < Inline open data 1 about here >

ERP component latencies were defined as the local peak latency between 100 and 190 ms for both bilateral and lateralised N1, between 140 and 230 ms for bilateral anterior P2, between 150 and 250 ms for lateralised N2pc, between 210 and 280 ms for bilateral anterior N2 and between 200 and 300 ms for bilateral N2pb. Mean amplitude measures of the peaks for each participant were taken in a 25 ms latency window around the peak of lateralised N1 (140.6 ± 2.0 ms), bilateral Anterior P2 (178.5 ± 4.0 ms), N2pc (204.3 ± 2.2 ms), bilateral Anterior N2 (240.6 ± 4.1 ms) and bilateral N2pb (247.9 ± 3.9 ms). Because latency measures can be highly sensitive to high-frequency noise, a low-pass filter prior to the latency measures (15 Hz, 12 dB/octave) was applied for each participant as in previous studies (Kappenman et al., 2016).

2.6 Statistical analysis

In all ANOVAs, Greenhouse–Geisser epsilon adjustments for non-sphericity were applied where appropriate. Post hoc paired *t*-tests were Bonferroni corrected for multiple comparisons.

2.6.1 Behavioural data

For each participant, only data for repeated trials (i.e. response mapping the same as the previous trial) with correct responses and RTs between 150 and 2000 ms, and also with values within three standard deviations from the individual's mean RT were analysed. RT and accuracy data were analysed with two repeated measures analyses of variance (ANOVAs).

Each ANOVA had two within-subjects factors: 'Session' (1, 2) and 'Trial Type' (match, mismatch trials).

2.6.2 ERP data

To test for any significant differences in the onset latency of both N2pc and MTN components, retrieved individual latencies of N2pc at PO7/8 electrodes were submitted to a paired sample t-test comparing session 1 and 2. Retrieved latencies of MTN were submitted to repeated measures ANOVA which had two within-subjects factors: 'Session' (1, 2) and rostro-caudal 'ROI' (FC, CP, PO).

The ANOVAs for both peak latencies and amplitudes of bilateral Anterior P2 and Anterior N2 components at FC ROI had two within-subjects factors: 'Session' (1, 2) and 'Trial Type' (Match, Mismatch trials). The ANOVAs for both peak latencies and amplitudes of the bilateral N2pb component at PO ROI had two within-subjects factors: 'Session' (1, 2) and 'Trial Type' (Match, Mismatch trials). The ANOVAs for both peak latency and amplitude of lateralised N1 at POL/R ROI had three within-subjects factors: 'Session' (1, 2), 'Trial Type' (Match, Mismatch trials), and 'Contralaterality' (Electrode Contralateral or Ipsilateral to the target). The ANOVAs for both peak latency and amplitude of the lateralised N2pc component at POL/R ROI had two within-subject factors: 'Session' (1, 2) and 'Trial Type' (Match, Mismatch trials). The mean amplitude of the N2pc component (time window 158-235 ms) was analysed with a two-way ANOVA with factors: 'Session' (1, 2) and 'Trial Type' (Match, Mismatch trial). The beginning and the end of the 77 ms time period analysed coincided with the onset (158 ms) and offset (235 ms) of N2pc statistically determined (see results section). The mean amplitude of the MTN component (time window 297-489 ms) was analysed with a three-way ANOVA with factors: 'Session' (1, 2), 'Sagittal Axis' (FC, CP, PO ROI) and 'Trial Type' (Match, Mismatch trial). The mean amplitude of mismatch-minus-

match trials difference waves was analysed with a two-way ANOVA with factors: ‘Session’ (1, 2) and ‘Sagittal Axis’ (FC, CP, PO ROI). The beginning and the end of the 192 ms time period analysed coincided with the onset (297 ms) and offset (489 ms) of MTN statistically determined (see results section).

2.6.3 Principal component analysis (PCA)

As mentioned earlier, PCA is a well-established analyses technique for highlighting hidden relations that explain the most variance in a dataset as a whole. Accordingly, the amplitudes of the ERP components collapsed across sessions described above (corresponding to our estimates of neurocognitive processes for each participant) were subjected to PCA for our dataset from 27 participants. One issue with PCA concerns the variable to subject ratio. Arrindell and van der Ende (1985) concluded that the cases-to variables ratio made little difference to the stability of factor solutions. One other issue with PCA concerns how many components to retain. The convention of setting the cut-off for retained eigenvalues at 1 has been criticised as too arbitrary (see Horn, 1965; O’Connor, 2000). Accordingly, here we followed the well-established “parallel analyses” procedure that has been shown to provide a more robust, statistically valid approach for resolving the number of components to retain from PCA (Horn, 1965; O’Connor, 2000). Thus, we implemented parallel analyses to yield a 95% confidence interval threshold (O’Connor, 2000) for 27 samples with 9 variables and 1000 datasets prior to the PCA on our experimental data. An SPSS syntax (Adapted from O’Connor, 2000) (http://global.oup.com/us/companion.websites/9780199734177/supplementary/factors/factors_a/) has been used to perform the parallel analyses. The actual PCA, using the correlation matrix of our experimental data, then used the eigenvalues thresholds as pre-set by the parallel analyses. As it turned out, three significant components were retained as above the eigenvalues thresholds derived from parallel analyses. In fact all three retained components’

eigenvalues were above one, and all further components below one. The retained components were Promax rotated in accord with the standard PCA approach.

2.6.4 Correlations

First, Pearson's product-moment correlations were computed on the whole sample of 27 individuals to investigate the relationship between behavioural (i.e. RTs and Accuracy) and electrophysiological (i.e. latencies and amplitude of ERP components) measures distinguished for trial types and sessions. Second, the modified version of the Pearson-Filon statistic (ZPF) (Raghunathan, Rosenthal, and Rubin 1996; Weaver and Wuensch, 2013) was used to assess the significance of the differences in the strength of correlation between the same two variables at two different time points, using the same sample. In particular, the ZPF statistic was computed between: i) behavioural and electrophysiological measures (e.g. comparing the correlation coefficient between mean RTs and mean amplitude of MTN at FC ROI for mismatch trials measured at Session 1 with the correlation coefficient between the same two variables measured at Session 2), and ii) ERP measures (e.g. comparing the correlation coefficient between mean onset latency of N2pc and mean onset latency of MTN at FC ROI measured at Session 1 with the correlation coefficient between the same two variables measured at Session 2). For further details of the procedure used to compare correlated but non-overlapping correlation coefficients using the ZPF statistic see Weaver and Wuensch (2013) and a Word file (<http://core.ecu.edu/psyc/wuenschk/StatHelp/ZPF.docx>). An SPSS syntax (<http://core.ecu.edu/psyc/wuenschk/SPSS/ZPF.sps>) has been used to perform the ZPF statistics.

3. Results

3.1 Behavioural results

As expected, participants responded more quickly after practice. There was a significant main effect of Session on RT $F_{(1, 26)} = 37.16, p < .0001, \eta_p^2 = .59$. Mean RT (\pm SE) was 833.4 ± 33.4 ms in session 1 and 759.3 ± 26.6 ms in session 2 with an average decrease of 124.1 ± 20.4 ms. There was a significant main effect of Trial Type $F_{(1, 26)} = 47.8, p < .0001, \eta_p^2 = .65$. RTs were significantly increased in mismatch compared to match trials in both session 1 (920.3 ± 34.1 ms vs 846.6 ± 33.6 ms, $p < 0.0001$) and session 2 (788.6 ± 28.9 ms vs 730.0 ± 25.3 ms, $p < 0.0001$; Fig. 2A1). The Session \times Trial Type interaction was non-significant, $F_{(1, 26)} = 1.63, p = .21, \eta_p^2 = .06$, showing that the magnitude of trial type effect on RT was similar comparing session 1 with session 2 (73.8 ± 10.9 ms vs. 58.6 ± 11.6 ms, $t_{(26)} = 1.28, p = \text{n.s.}$; Fig. 2A2).

As expected, participants were more accurate in their responses after practice. There was a significant main effect of Session on Accuracy $F_{(1, 26)} = 20.28, p < .001, \eta_p^2 = .44$. Mean Accuracy (\pm SE) was 82.8 ± 1.8 % in session 1 and 87.1 ± 1.7 % in session 2 with an average increase of 4.3 ± 0.9 %. There was a significant main effect of Trial Type $F_{(1, 26)} = 27.0, p < .00001, \eta_p^2 = .51$. Mean Accuracy was 81.8 ± 1.9 % in session 1 and 88.1 ± 1.7 % in session 2 with an average increase of 6.3 ± 1.2 %; Fig. 2B1. Critically, there was a significant Session \times Trial Type interaction, $F_{(1, 26)} = 5.58, p = .026, \eta_p^2 = .18$. Post-hoc pairwise comparisons revealed that accuracy was significantly increased in match compared to mismatch trials in both session 1 (86.7 ± 1.8 % vs. 79.0 ± 2.1 %, $p < .0001$) and session 2 (89.5 ± 1.7 vs 84.6 ± 1.9 , $p < 0.001$). This facilitation effect for match trials as compared to mismatch trials was significantly reduced by 2.8 ± 1.2 % comparing session 1 with session 2 (7.7 ± 1.5 vs. 4.9 ± 1.1 , $t_{(26)} = 2.36, p = .026$; Fig. 2B2).

< Figure 2 about here >

3.2 Electrophysiological results

Table 1 summarises the main findings of modulation of each of the ERP components with practice.

< Table 1 about here >

3.2.1 Early visual sensory processing: N1

Statistical analyses on the mean (\pm SE) latency of the lateralised N1 peak at POL/R ROIs (140.1 ± 2.0 ms) revealed an overall significant main effect of Session, $F_{(1, 26)} = 4.51$, $p = .043$, $\eta_p^2 = .15$. Mean latency was 141.5 ± 2.1 ms in session 1 and 138.6 ± 2.1 ms in session 2 with an average reduction of 2.8 ± 1.3 ms. Fig. 4A–B shows grand averages of waveforms at POL/R ROIs for contralateral and ipsilateral sites relative to the target in Session 1 and Session 2. There was also a main effect of Contralaterality, $F_{(1, 26)} = 5.23$, $p = .031$, $\eta_p^2 = .17$. Mean latency was increased for sites contralateral to the target compared with ipsilateral sites (140.7 ± 2.1 ms vs 139.4 ± 1.9 ms) with an average increase of 1.4 ± 0.6 ms.

< Figure 3 about here > < Figure 4 about here >

Statistical analyses on mean amplitudes around the lateralised N1 peak at POL/R ROIs revealed no significant main effects or interactions. Overall the significant results suggest an enhancement of neural responses to the stimulus arrays with practice.

3.2.2 Detection of a specific pop-out feature: Anterior P2

Statistical analyses on mean (\pm SE) latency of bilateral Anterior P2 peak at FC ROI (178.5 ± 4.1 ms) revealed a significant main effect of Session $F_{(1, 26)} = 6.14$, $p = .020$, $\eta_p^2 = .19$. Mean latency was 182.0 ± 4.0 ms in session 1 and 175.0 ± 4.7 ms in session 2 with

an average reduction of 7.0 ± 2.8 ms. Statistical analyses on mean amplitudes around the bilateral anterior P2 peak revealed no significant main effects or interactions. These results indicate earlier detection of a specific pop-out feature with practice. Grand average of bilateral ERP waveforms at FC ROI are shown in Fig. 3A1.

3.2.3 *Focusing Covert Attention on a Peripheral Location: N2pc*

To isolate the N2pc component from the overlapping bilateral ERP components and directly compare the magnitude of the N2pc between the two Sessions, contralateral-minus-ipsilateral difference waves were computed (Fig. 4C). The N2pc onset latency, peak latency, mean amplitude around the peak and mean amplitude in the time window 158-235 ms post-stimulus onset were measured from these waveforms. For both Session 1 and Session 2, the N2pc component can be seen as a more negative (i.e. less positive) contralateral voltage beginning at approximately 150 ms post-stimulus during visual search. Collapsing the difference ERP waveforms across all participants, Sessions, Trial Types, N2pc onset time was at 158 ms ($t_{(26)} = -2.93, p < .01$) whereas its offset was at 235 ms ($t_{(26)} = -2.97, p < .01$) post stimulus onset. As predicted, the paired t-test on retrieved onset latencies of N2pc comparing session 1 (161.2 ± 4.4) and session 2 (152.5 ± 3.1) was significant $t_{(26)} = 1.188, p = .035$ (1-tailed). These results demonstrate that the time required for the initial shift of attention to be reliably focused on the target, decreased by 8.8 ± 4.7 ms after practice. However statistical analyses on mean (\pm SE) latency of the lateralised N2pc peak at POL/R ROIs (204.2 ± 2.2 ms) revealed no significant main effects or interactions.

Interestingly, the mean (\pm SE) amplitude around the lateralised N2pc peak at POL/R ROIs appears substantially more negative in Session 2. These observations were substantiated by statistical analyses. There was a significant main effect of Session $F_{(1, 26)} = 16.24, p < .001, \eta^2 = .38$. Mean amplitude around the peak was -1.68 ± 0.18 μ V in session 1 and -

2.16 \pm 0.20 μ V in session 2 with an overall more negative amplitude of -0.48 \pm 0.12 μ V.

Further confirmation of these significant results came from the statistical analyses of mean amplitude of N2pc at POL/R ROIs (time window 158-235 ms) which revealed a significant main effect of Session, $F_{(1, 26)} = 18.25$, $p < .001$, $\eta_p^2 = .41$. Mean amplitude in the statistically defined time window was -1.19 \pm 0.15 μ V in session 1 and -1.61 \pm 0.16 μ V in session 2 with an overall more negative amplitude of -0.42 \pm 0.10 μ V. Overall these significant results suggest an improvement in the process of orienting and focusing covert attention on peripheral target features with practice.

3.2.4 *Detection of conflicting pop-out features: Anterior N2*

Statistical analyses on mean (\pm SE) latency of the bilateral anterior N2 (or N270) peak at FC ROI (240.3 \pm 4.5 ms) revealed no significant main effects or interactions. Whereas statistical analyses of the mean (\pm SE) amplitudes around the bilateral anterior N2 peak at FC ROI showed a significant Session x Trial Type interaction $F_{(1, 26)} = 5.09$, $p = .03$, $\eta_p^2 = .16$. Post-hoc pairwise comparisons revealed that N2 amplitude for mismatch trials was significantly more negative in Session 2 than Session 1 (-1.69 \pm 0.51 μ V vs -0.51 \pm 0.56 μ V, $p = .03$) with an average difference of 1.18 \pm 0.50 μ V. Moreover for session 2 only, the N2 amplitude was significantly more negative for mismatch trials than match trials (-1.69 \pm 0.51 μ V vs -1.16 \pm 0.48 μ V; $p = .03$). These mismatch trials effect results suggest that detection of conflicting features is enhanced with practice.

3.2.5 *Categorisation of stimuli: Posterior N2pb*

Statistical analyses on mean (\pm SE) latency of the bilateral N2pb peak at PO ROI (247.7 \pm 4.0 ms) revealed no significant main effects or interactions. The mean (\pm SE) amplitude around the bilateral N2pb peak at PO ROI appears substantially reduced in Session

2. These observations were substantiated by statistical analyses. There was a significant main effect of Session $F_{(1, 26)} = 10.47, p < .005, \eta^2 = .29$. Mean amplitude was $-1.23 \pm 0.74 \mu\text{V}$ in session 1 and $-0.08 \pm 0.82 \mu\text{V}$ in session 2 with an overall amplitude attenuation of $-1.15 \pm 0.35 \mu\text{V}$. These results suggest that specific pop-out target features were more easily categorised with practice.

3.2.6 Integration of STVM representations: MTN component

Fig. 3A1-B1-C1 shows separate waveforms for match and mismatch trials at FC, CP and PO ROIs respectively. For both sessions, the MTN component can be seen as a more negative (i.e. less positive) voltage for mismatch trials starting at about 300 ms and lasting up to 550 ms post-stimulus at all ROIs as in a previous study (Fuggetta et al., 2015). In order to directly compare the magnitude of MTN between ROIs, mismatch-minus-match trials difference waves were computed as shown in Fig. 3A2-B2-C2. Collapsing the difference ERP waveforms across all participants, Sessions, Trial Types and ROIs, MTN onset time was at 297 ms ($t_{(26)} = -2.84, p < .01$) whereas its offset was at 489 ms ($t_{(26)} = -2.88, p < .01$) post stimulus onset. The ANOVA conducted to test the difference in MTN onset latency between Session 1 and Session 2 revealed a significant main effect of ROI $F_{(1.6, 41.6)} = 10.62, p < .001, \eta^2 = .31$. There was also a significant ROI x Session interaction $F_{(1.5, 39.5)} = 5.79, p < .05, \eta^2 = .19$. Post-hoc pairwise comparisons revealed that in the case of FC ROI onset latency of MTN was substantially reduced in Session 2 than Session 1 (232.9 ± 13.4 ms vs 289.8 ± 8.6 ms, $p < .005$). On the contrary there was no significant difference in onset latency of MTN comparing the two sessions for CP (292.4 ± 12.4 ms vs 293.5 ± 10.5 ms, $p = \text{ns}$) and PO (317.2 ± 12.8 ms vs 305.6 ± 15.0 ms, $p = \text{ns}$) ROIs. These results demonstrate that the time to integrate the visual representation of the target with the existing features of cue shape

available in STVM was significantly earlier with an average decrease of 56.9 ± 18.0 ms at FC ROI with practice.

Statistical analyses on the mean amplitude of MTN (time window 297-489 ms) revealed a significant Session x ROI interaction, $F_{(1.4, 36.9)} = 26.51, p < .0001, \eta_p^2 = .50$. Post-hoc pairwise comparisons revealed that in the case of FC ROI and trial types the voltage of the MTN was more negative (i.e. less positive) in Session 2 than Session 1 ($2.58 \pm 0.49 \mu\text{V}$ vs $3.34 \pm 0.48 \mu\text{V}, p = .04$). Whereas, in the case of for PO ROI, this component was significantly less negative (i.e. more positive) in Session 2 than Session 1 ($5.90 \pm 0.68 \mu\text{V}$ vs $4.60 \pm 0.70 \mu\text{V}, p < .005$). There was also a ROI x Trial Type interaction $F_{(1.1, 29.5)} = 4.78, p = .03, \eta_p^2 = .15$. Post-hoc pairwise comparisons revealed that the magnitude of the MTN component extended to all ROIs but was also significantly different between them. In particular, the MTN was of $-1.52 \pm 0.25 \mu\text{V}$ ($p < .0001$) for FC ROI, of $-1.81 \pm 0.21 \mu\text{V}$ ($p < .0001$) for CP ROI, and of $-1.05 \pm 0.23 \mu\text{V}$ ($p < .0001$) for PO ROI. Indeed statistical analyses of the mean amplitude of mismatch-minus-match trials difference waves (time window 297-489 ms) revealed a significant main effect of ROI $F_{(1.1, 29.5)} = 4.78, p = .03, \eta_p^2 = .15$. Post-hoc pairwise comparisons revealed that the magnitude of MTN component was substantially larger in CP as compared to PO ROI (-1.81 vs. $-1.05 \mu\text{V}, p < 0.001$).

3.3 Principal component analysis (PCA)

Based on the parallel analyses for 27 samples with 9 variables, eigenvalue thresholds (95% upper confidence limit of the distribution of eigenvalues derived from the random data in the parallel analyses) for retaining each successive component from a maximum of nine successive components were: 2.33, 1.83, 1.52, 1.26, 1.05, .87, .69, .55, and .38. The actual resulting eigenvalues for successive components from the PCA of the amplitude of ERP dataset were 3.43, 1.93, 1.60, .82, .60, .41, .15, .06, and .01. Accordingly just the first three

principal components were retained as above the threshold determined by the parallel analyses, and were then subjected to Promax rotation. The Kaiser-Meyer-Olkin measure of sampling adequacy was .53. A value greater than .5 has been recommended as being barely acceptable Kaiser (1974), indicating that patterns of correlations are relatively compact and so PCA should yield distinct and reliable factors. The Bartlett's test of sphericity was significant $\chi^2_{(36)} = 212.8, p < .001$, indicating that the correlations between variables were overall significantly different from zero.

Remarkably, each of the three principal components obtained turned out to have different rostro-caudal topographic representations. As shown by the bold values in Table 2, the first component included both the centro-parietal and parieto-occipital MTN, which loaded with second negative posterior-bilateral (N2pb) component. The second component comprised the amplitude of bilateral anterior P2, which loaded with bilateral anterior N2, and fronto-central MTN. Lastly, the third component included the ipsilateral and contralateral parieto-occipital N1, which loaded with second negative posterior-contralateral (N2pc) component. The first principal component explained 38.1% of the variance; the second 21.5%; and the third 17.8%. So cumulatively these three components we retained accounted for 77.3% of the variance in electrophysiological data. Reliability statistics were performed on each of the three extracted components. Cronbach's alpha was .79, .77 and .80, for first second and third component, demonstrating acceptable internal consistency.

< Table 2 about here >

3.4 Correlations

Significant results of statistical analyses performed to assess the strength of correlation between behavioural and electrophysiological measures, and between electrophysiological measures comparing the first with the second session are shown in Table 3. Supplementary

Fig. S1 also shows the scatter plots of correlations between pairs of two variables at session 1 and session 2.

< Table 3 about here > < Supplementary Figure S1 about here >

Taking onto account the comparison of correlation coefficients between behavioural and electrophysiological measures, the outputs show that the degree of association between mean accuracy and mean amplitude of N2pc for mismatch trials was significantly lower at the time of the second session than at the time of the first session (See Table 3, comparison A and Supplementary Fig. S1, panels A1-A2). Furthermore, the correlations between mean RTs with both peak latency and amplitude of N2pb for both match and mismatch trials were significantly higher at the time of the second session than at the time of the first session (See Table 3, comparisons B-D and Supplementary Fig. S1, panels B1-D2). ZFP statistics also revealed that correlations between mean RTs and both onset latency of MTN at FC ROI and mean amplitude of MTN at FC, CP and PO ROIs were significantly higher at the time of the second session than at the time of the first session (See Table 3, comparisons E-I and Supplementary Fig. S1, panels E1-I2).

Assessments of the modulation of correlation coefficients between electrophysiological measures with practice show that the degree of association between mean onset latency of N2pc with onset latency of MTN at FC ROI was significantly higher at the time of the second session than at the time of the first session (See Table 3, comparison J and Supplementary Fig. S1, panels J1-J2). This significant result is further supported by the significantly lower degree of association between onset latency of MTN of FC with CP ROI at the time of the second session than at the time of the first session (See Table 3, comparison K and Supplementary Fig. S1, panels K1-K2). Lastly, there was a significantly higher correlation between peak latency of N2pc with peak latency of bilateral N1 for match trials at the time of

the second session than at the time of the first session (See Table 3, comparison L and Supplementary Fig. S1, panels L1-L2).

4 Discussion

The main purpose of the study was to determine which neurocognitive stages involved in the operation of attention to visible objects (i.e. covert visual spatial attention, feature-based attention and the process of integration with representations in STVM) (Luck, 2012; Luck and Kappenman, 2012) underlie the improvement of behavioural performance with practice. To this end, we adopted an experimental design which combines two paradigms within the context of a single experiment: a delayed match-to-sample task (Wang et al., 2004; Wang et al., 2003) with a memory guided efficient pop-out visual search paradigm (Treisman and Gelade, 1980) within the same trial sequence (Bennett et al., 2014; Fuggetta et al., 2015) in two-day recording sessions one week apart. Participants completed 20 minutes of training prior to each of the two experimental recording sessions which lasted 60 minutes each. These training periods were necessary for participants to become familiar with the cognitive task and reduce the risk that some of them performed the experimental task at chance level.

Luck and Gold (2008) provided a conceptual framework for attention which can be applied to the current experimental paradigm as follows. When the cue shape (S1) appeared, participants stored its identity (i.e. colour and shape) in STVM. Then executive processes both set and sent parameters to the input selection system that determined what types of inputs should be selected for the combined visual search and match-to-sample task. Thus these parameters caused attention to be guided to the relevant-features of the to-be detected target shape (S2). This process is termed control of selection in Luck & Gold's (2008) framework. The input selection process in turn caused attention to focus on the target,

1 facilitating processing of the attended target's features such as colour and shape, and
2 inhibiting processing of the unattended distractor inputs. This process is termed
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4 implementation of selection in Luck & Gold's (2008) framework. The purpose of using a
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6 feature 'pop-out' search array of homogeneous distractors (Treisman and Gelade, 1980) in
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8 the current study, was to make the implementation of selection easy, providing high-fidelity
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10 perceptual-related ERP components with minimum trial-to-trial timing variability as in
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12 previous studies (Bennett et al., 2014; Clark et al., 2015; Fuggetta et al., 2015; Luck et al.,
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15 1994).

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20 Our task involved a high-level of attentional control processes as it included an STVM
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22 component that may have strained the attentional system to which it is linked. Thus it is
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24 plausible that these factors may have stressed the implementation of selection process more
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26 than in previous studies which have investigated practice-related changes in visual search
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28 using conjunction search (An et al., 2012; Hamame et al., 2011) or feature pop-out search
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30 (Clark et al., 2015). Furthermore those studies have primarily assessed ERP components from
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32 parieto-occipital electrode sites (i.e. N1, N2pc, SPCN), whereas the current study also
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34 investigated attention-related ERP components recorded at frontal-central (i.e. Anterior P2,
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36 Anterior N2 and MTN) sites to obtain a more comprehensive view of the cascade of attention
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38 mechanisms that may change as a result of practice. Table 1 summarises the main effect of
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40 practice on modulation of the six ERP components that have been analysed.
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50 *4.1 Early visual sensory processing: N1*

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52 After practice, we observed a slight but significant latency reduction (~3 ms) in the
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54 lateralised N1 (latency ~140 ms) sensory component at PO ROI, indicating that speeding of
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56 basic visual sensory processing contributes to the faster and more accurate performance with
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58 practice. Contrary to our findings, a previous study using a feature-singleton target-popout
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task did not observe a change in the latency of the N1 component after practice (Clark et al., 2015). This difference between the two studies might be related to the greater number of participants in the current study compared with the previous investigation (27 vs. 19) which enhanced the statistical power of the current study. We also found a small degree of contralaterality of the early sensory-evoked N1 component: latencies for sites contralateral to the target were slightly increased, but we did not find a significant practice outcome on this effect. We did, however, observe a significant lateralised increase in the amplitude of the N1 component, contralateral to the target at POL/R electrode sites after practice. The result on latency of N1 suggests that practice enhanced early sensory responses to the entire array, as discussed in a previous study (Clark et al., 2015). This result confirms a cortical reorganisation (i.e. plasticity) at this early sensory processing stage in the case of a feature-singleton target-pop-out task (Clark et al., 2015). The effect of practice on N1 laterality which is likely related to the low-level feature analyses including the early part of the contralaterality of N2pc, which began in the middle of the N1 latency range (see below).

4.2 Detection of a specific pop-out feature: Anterior P2

After practice, we observed a significant latency reduction (~7 ms) in the bilateral anterior P2 component (latency ~179 ms) at FC ROI, indicating that the process of detecting a specific target pop-out feature (Luck and Hillyard, 1994a, b) was speeded. This likely contributes to the faster and more accurate performance with practice. We did not, however observe a significant bilateral increase in the amplitude of the anterior P2 after practice. This indicates that speeding of the process of detecting a specific pop-out feature is not associated with greater intervention of feature-based attention towards the relevant feature.

4.3 Focusing Covert Attention on a Peripheral Location: N2pc

The N2pc (latency ~204 ms) reflects a lateralised shifting and focusing of attention to a specific target item (Hopf et al., 2000; Luck et al., 2006). We found that onset latency for the early phase of the N2pc component was reduced in Session 2 by ~ 9 ms. This demonstrates that the time required for the initial shift of attention to be reliably focused on the target, was significantly reduced with practice. This process reflects the activation of parietal areas to initiate a rapid shift of attention towards the task-relevant target location (Corbetta et al., 1995; Fuggetta et al., 2006; Hopf et al., 2000) and suggests that the control of input selection as defined by Luck and Gold's (2008) framework can be improved with training. This finding is consistent with a recent study examining practice (Clark et al., 2015), which also reported a significant reduction in the onset latency of the N2pc component after practice, using a feature-singleton target-pop-out task.

Further, we observed a larger amplitude of the N2pc peak and larger mean amplitude at POL/R ROIs with practice. This indicates enhanced amplitude of the late phase of the N2pc component, which is implemented by extrastriate areas of the occipital and inferior temporal cortex (Hopf et al., 2006; Hopf et al., 2000). This suggests an enhancement in the implementation of selection – referring to the process that enhances the task-relevant features of target and suppresses the irrelevant inputs – with practice (Luck, 2012; Luck and Gold, 2008). This result is consistent with the results of three studies examining practice with both conjunction visual search (An et al., 2012; Hamame et al., 2011) and feature-singleton target-pop-out task (Clark et al., 2015), which also reported a larger N2pc after practice.

4.4 Detection of conflicting pop-out features: Anterior N2

The anterior N2 (or N270) (latency ~240 ms) amplitude for mismatch trials was significantly larger with practice. This component reflects processing of information which mismatches with representations in STVM in a delayed match-to-sample task where S2 and S1 could differ on two dimensions: colour and shape (Wang et al., 2004). In three different tasks, participants were asked to indicate if S2 matched S1 on colour, shape and on both features. It was found that when participants attended to both colour and shape and S2 differed from S1 on both these features, both the N270 and a later component named N400 were present, suggesting that these two components reflect sequential processing of two mismatches (Wang et al., 2004). A previous study from our lab (Bennett et al., 2014) used a paradigm combining a match-to-sample task, with a memory-guided efficient popout visual-search with homogenous distractors within the same trial sequence, as in the current study, to investigate whether adding distractors to S2 could affect the N270 because the distractors are a source of task-irrelevant mismatch. Both a negativity between 250-299 ms (N270) and a negativity peaking around 400 ms (MTN) were found. We suggested the possibility that these two negativities reflected sequential processing of two mismatches, the first being a mismatch between S1 and the distractors and the second one between S2 and S1 (Bennett et al., 2014). Thus in the current study, we propose that the presence of the anterior N2 (or N270) and the MTN is the result of a sequential comparison process between STVM representations of S1 with those of the distractors (task-irrelevant mismatch) and target (task-relevant mismatch) in S2.

In the present study, the finding of an enhanced anterior N2 in Session 2 suggests that detection of conflicting features between the shape cue (S1) and the target array of homogenous distractors (S2) is enhanced through practice. This process is likely related to the

analyses including the early part of the MTN. Zhang et al., (2008) used fMRI to investigate the locus of the N270 in a delayed match-to-sample task. Subjects were required to indicate if S2 matched S1 on one feature dimension (i.e. shape) during both an ERP and a functional magnetic resonance imaging (fMRI) session. The authors found that mismatching shapes evoked the N270 (ERP session) and that the right anterior cingulate cortex (ACC) and the right dorsolateral prefrontal cortex (DLPFC) were more active on mismatch trials (fMRI session). These findings are in line with evidence of a conflict-monitoring system in the ACC acting in association with a DLPFC implementing cognitive control (Botvinick et al., 2001).

4.5 Categorisation of stimuli: Posterior N2pb

The mean amplitude around the bilateral N2pb peak (latency ~248 ms) at PO ROI was substantially reduced with practice. In a previous study it was found that the N2pb is enlarged for target pop-outs compared to nontarget pop-outs, it varies with target probability and is larger for colour pop-outs than for orientation or size pop-outs (Luck and Hillyard, 1994a). Renault et al., (1982) proposed that this component reflects the process of categorising a stimulus, because the enlargement of this component depends on the difficulty of the categorisation. Accordingly, our results of a reduced amplitude of N2pb component likely reflects learning for the hexagon-diamond discrimination of the pop-out target such that it became less demanding after practice. Therefore it seems that a specific pop-out target's features were more easily detected and categorised, requiring a reduced intervention of feature-based attention towards the task-relevant features with practice, which is likely related to the analyses including a reduction of the MTN at PO ROI (see below).

4.6 Integration of STVM representations: MTN component

In the current study, an enhanced MTN (latency 297-489 ms) was observed at all ROIs found in both sessions as in previous studies (Bennett et al., 2014; Fuggetta et al., 2015). Enhanced MTN has been previously interpreted as reflecting post-perceptual operation of executive functions to integrate the task-relevant post-perceptual memory representation of the currently encoded target (S2) with the conflicting representation of the initial cue (S1) held in STVM (Fuggetta et al., 2015).

In the current study, the onset latency of MTN, defined as the difference in amplitude between mismatch and match trial waveforms, was shortened by ~57 ms in Session 2 compared to Session 1 at FC ROI. This result suggests that the time to integrate the visual representation of the target with the features of the cue shape in STVM was significantly reduced with practice. Furthermore, we found that the mean amplitude of both match/mismatch trials in the time window of MTN (297-489 ms after the target array) increased over the two sessions. In particular, we observed relatively more negative (i.e. less positive) waveforms at FC ROI. This enhanced response to conflict suggests that the process of integrating perceptual representations with a conflicting representation held in STVM is performed more effectively with practice.

Moreover, within the time window of MTN (297-489 ms after the target array), there were less negative waveforms for both match and mismatch trials at PO ROI with practice. A similar effect was reported by Clark et al. (2015). They found a substantial decrease in the amplitude of SPCN (340-480 ms after stimulus array) after practice. The authors explained their findings as reflecting an enhancement of pop-out target discrimination, which became less demanding through practice (Clark et al., 2015). Likewise, in the current study, the

reduction of MTN at PO ROI after practice may reflect the maintaining of less demanding visual information in working memory.

4.7 Principal component analysis (PCA)

PCA revealed the existence of three major components in our ERP data, as shown by the bold values in Table 2. The first component included both the centro-parietal and parieto-occipital MTN, involved in integrating visual representations of the target with the task-relevant existing representations stored in visual working memory, which loaded with second negative posterior-bilateral (N2pb) component, related with categorisation of specific pop-out target features. Taking into account the Luck and Gold's (2008) framework, the functional significance of this component could be related to the implementation of selection process where executive control parameters are sent to the categorisation and motor systems which make a same/different shape judgment in a match-to-sample task.

The second component comprised the amplitude of bilateral anterior P2, related to the detection of a specific pop-out feature, which loaded with bilateral anterior N2, associated with detection of conflicting features, and fronto-central MTN. Overall this component highlighted by PCA seems to be involved in the control of selection (i.e. the process of determining which inputs will be selected) as defined by the Luck and Gold's (2008) theory. In the case of the match-to-sample combined with visual search paradigm employed in this study, when the to-be-attended cue changes from trial-to-trial, the control of selection process involves monitoring and evaluating which cue features need to be stored in working memory. Consequently, working memory provides a bias signal that influences input selection of target objects matching the cue's representations (Woodman, Luck and Shall, 2007, Desimone and Duncan, 1995).

Lastly, the third component included the ipsilateral and contralateral parieto-occipital

1 N1, related to early neural responses to the stimulus array, which loaded with the second
2 negative posterior-contralateral (N2pc) component, which mediates the process of orienting
3 and focusing covert attention on peripheral target features. The functional significance of this
4 component could also be part of the implementation of selection process where after the
5 initial recognition of perceptual features of objects that should be selected, an enhancement of
6 the processing of the relevant input and suppression of irrelevant input takes place.
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15 *4.8 Correlations*

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17 We found that improvements in behavioural performance with practice (RT reduced by
18 ~124 ms and accuracy improved by ~ 4 %) occurred in parallel with several changes in the
19 neural activity associated with electrophysiological measures. However it is difficult to define
20 which ERP components have primarily contributed to the changes of behavioural
21 performance observed with practice. In order to resolve this matter, we evaluated the
22 modulation of correlation coefficients between behavioural and electrophysiological
23 measures at two different moments in time.
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37 Statistical analyses of correlation coefficients between behavioural data and ERP
38 components revealed a significant increased negative association between improved accuracy
39 in performing the task and more negative N2pc with practice. Furthermore, a significant
40 increased positive association was found between faster RTs and both latency and amplitude
41 of N2pb and earlier and more negative (less positive) MTN with practice. These results
42 suggest that the N2pc, N2pb and MTN represent the main electrophysiological contributors
43 to the improvement of behavioural performance observed with practice.
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55 The comparison of correlation coefficients between electrophysiological measures
56 revealed a significantly increased positive association between earlier onset of N2pc with
57 earlier onset of MTN at FC ROI (but not at CP ROI) with practice. Also, a significantly
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increased link was found between onset of N2pc (i.e. selection time) and latency of N1 component with practice. These complementary results provide further evidence that both the N2pc and MTN represent two fundamental ERP components which enhanced the links between VSTM, visual attention and cognitive control processes and led to a more rapid and efficient motor-response selection and execution, as reflected by the faster response time and increased accuracy after practice.

5. Conclusions

The current study assessed the temporal and functional organization of cognitive processes, to elucidate neural mechanisms involved in improvements in visual cognition with practice. In particular, we investigated the neural networks of visual object recognition and the link between STVM, cognitive control and visual attention processes asking participants to perform an input selection task. We examined the effect of practice on a series of electrophysiological markers underlying perceptual and post-perceptual processes. Correlation results revealed that practice had a strong impact on the ERP components of N2pc, reflecting the process of orienting and focusing covert attention on peripheral target features (Luck et al., 2006; Luck et al., 1994) and MTN, reflecting the integration of task-relevant memory representation of the currently encoded target with representation of the initial cue held in STVM (Fuggetta et al., 2015). Furthermore the effect of practice also improved the regional connectivity of the ERP components N1 and N2pc at PO ROI and the cortico-cortical interaction between PO and FC ROI, enhancing the strength of correlation between N2pc and MTN at FC ROI, most likely facilitating the executive control role (i.e. categorisation process) to be applied more efficiently in performing the match-to sample task.

Overall, the results of this electrophysiological study provide further support for the hypothesis that practice-induced changes in neural mechanisms underlie learning (Clark et al., 2015). The novelty of the paper, and its main contribution, is that by combining existing paradigms we have been able to assess a wider range of markers in a single study than in previous studies. The main result is that all of the markers indicate improvement with practice. The implications of the present findings can serve to motivate further research aimed at exploring how the combination of a series of paradigms from Experimental Psychology / Cognitive Neuroscience, could lead to an enhancement of both behavioural performance and neural responses throughout task-engaged cortical regions with practice.

Contributors

G. Fuggetta was responsible for all aspects of study design, data collection, experimental methods, signal analyses, statistical analysis, data interpretation, and manuscript preparation. P. Duke was responsible of programming the task, experimental methods, and manuscript preparation. All authors contributed to and approved the final manuscript.

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Figure and tables captions

Fig. 1. Example of a sequence of events of one trial of the experiment. (A) Shape Cue; (B) Fixation; (C) Informative Cue; (D) Delay; (E) Target Array; (F) Response. Subjects' task was to indicate whether the informative cue shape (C) matched or mismatched the target array shape (E). This trial is an example of match condition because the cue shape (S1) is same from the target shape (S2).

Fig. 2. Behavioural results. The mean RT (A1), difference values of RT (Mismatch trials – Match trials) (A2), mean accuracy (B1) and difference values of accuracy (Match trials – Mismatch trials) (B2) are shown across the sessions. Error bars represent (\pm SEM). The response time decreased significantly after practice (A1), but the magnitude of trial type effect on RT, with faster responses for match trials, was similar across the sessions (A2). The accuracy increased significantly after practice (B1), and the facilitation effect for match trials as compared to mismatch trials was significantly reduced with practice (B2). *** $p < .001$; * $p < .05$.

Fig. 3. Grand average ERP bilateral waveforms separated by match and mismatch trials averaged across fronto-central (A1), centro-parietal (B1), and parieto-occipital (C1) ROIs. Grand average mismatch-minus-match difference waveforms averaged across fronto-central (A2), centro-parietal (B2); and parieto-occipital (C2) ROIs. Comparing the two sessions the bilateral ERP components of Anterior P2, Anterior N2 (or N270), N1, N2pb and mismatch-triggered negativity were modulated after practice (See text for further details). Vertical lines in A2, B2 and C2 indicate the onset of post-perceptual mismatch-triggered negativity (MTN) component across sessions.

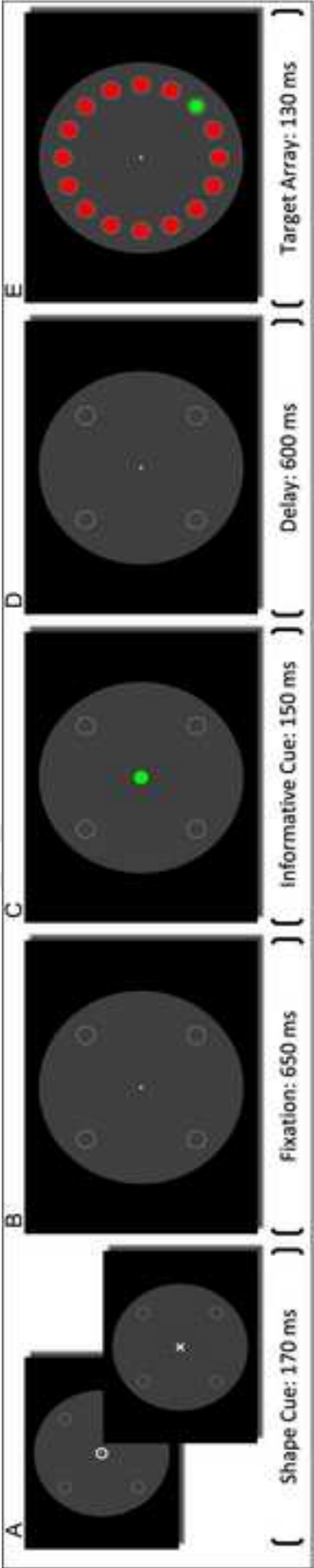
Fig. 4. Grand average ERP lateralised waveforms from experiment at parieto-occipital ROI in session 1(A) and session 2 (B). Contralateral waveforms were computed by averaging left-target waveforms at right-hemisphere electrode sites with right-target waveforms at left-hemisphere electrode sites. Ipsilateral waveforms were computed by averaging left-target waveforms at left-hemisphere electrode sites with right-target waveforms at right-hemisphere electrode sites. (C) Grand average contralateral-minus-ipsilateral difference waveforms, averaged across the left and right parieto-occipital ROIs. Comparing the two sessions the lateralised ERP components of N1 and N2pc were modulated after practice (See text for further details). Vertical lines in C indicate the onset of N2pc component for match trials and mismatch trials across sessions.

Supplementary Fig. S1. Scatter plots of correlations between pairs of two variables at session 1 and session 2.

Table 1. Summary of the main effect of practice on latency and amplitude of ERP components (N=27).

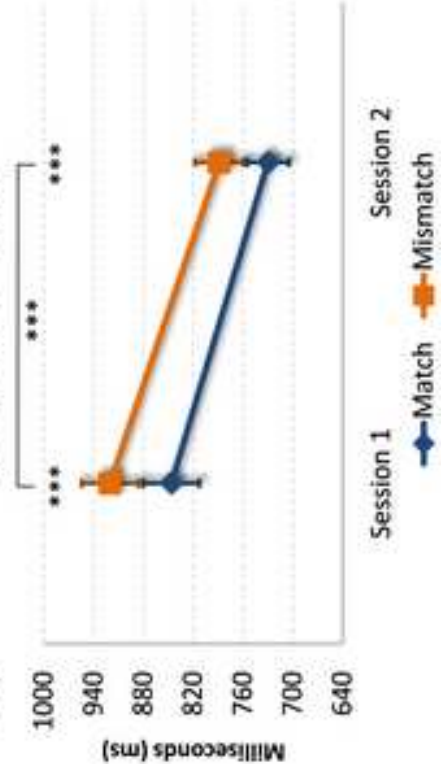
Table 2. Loadings on each of the three principal components retained from the PCA on average of ERP amplitudes collapsed across sessions, as determined by thresholds from the parallel analyses, shown after Promax rotation. Large loadings have been highlighted in bold to emphasize the variables that contribute to each principal component. Communalities have been also reported (N = 27).

Table 3. Pearson's product-moment correlations and modified Pearson-Filon (ZPF) test results comparing correlation coefficients between two variables at two different time points ($N = 27$).

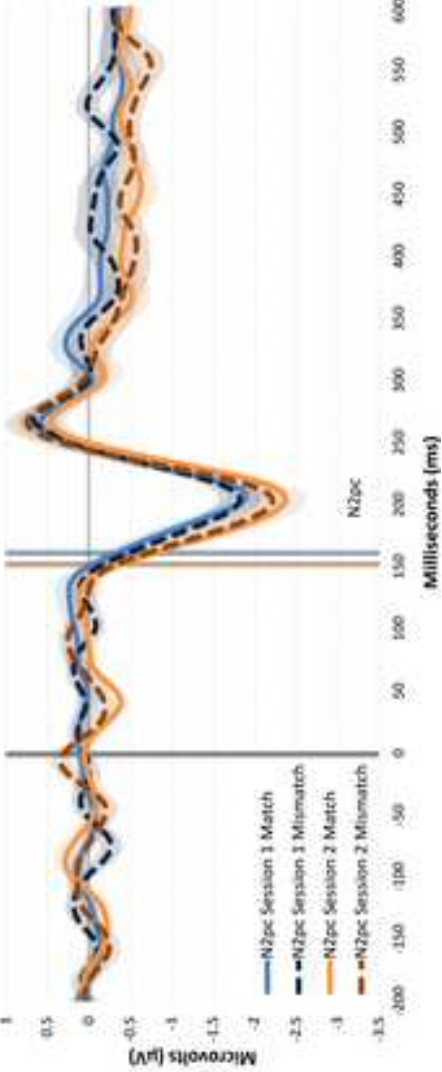


A1

Response Time

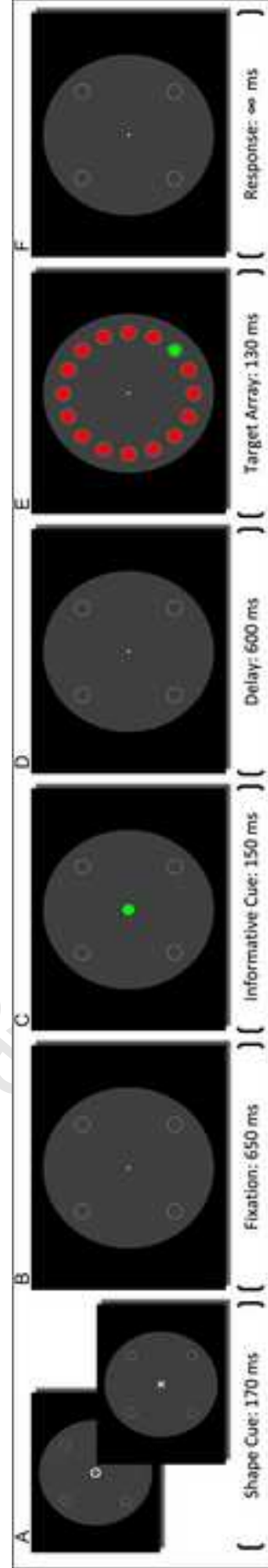


ERPs of Difference (Contralateral - Ipsilateral) at POL/R sites

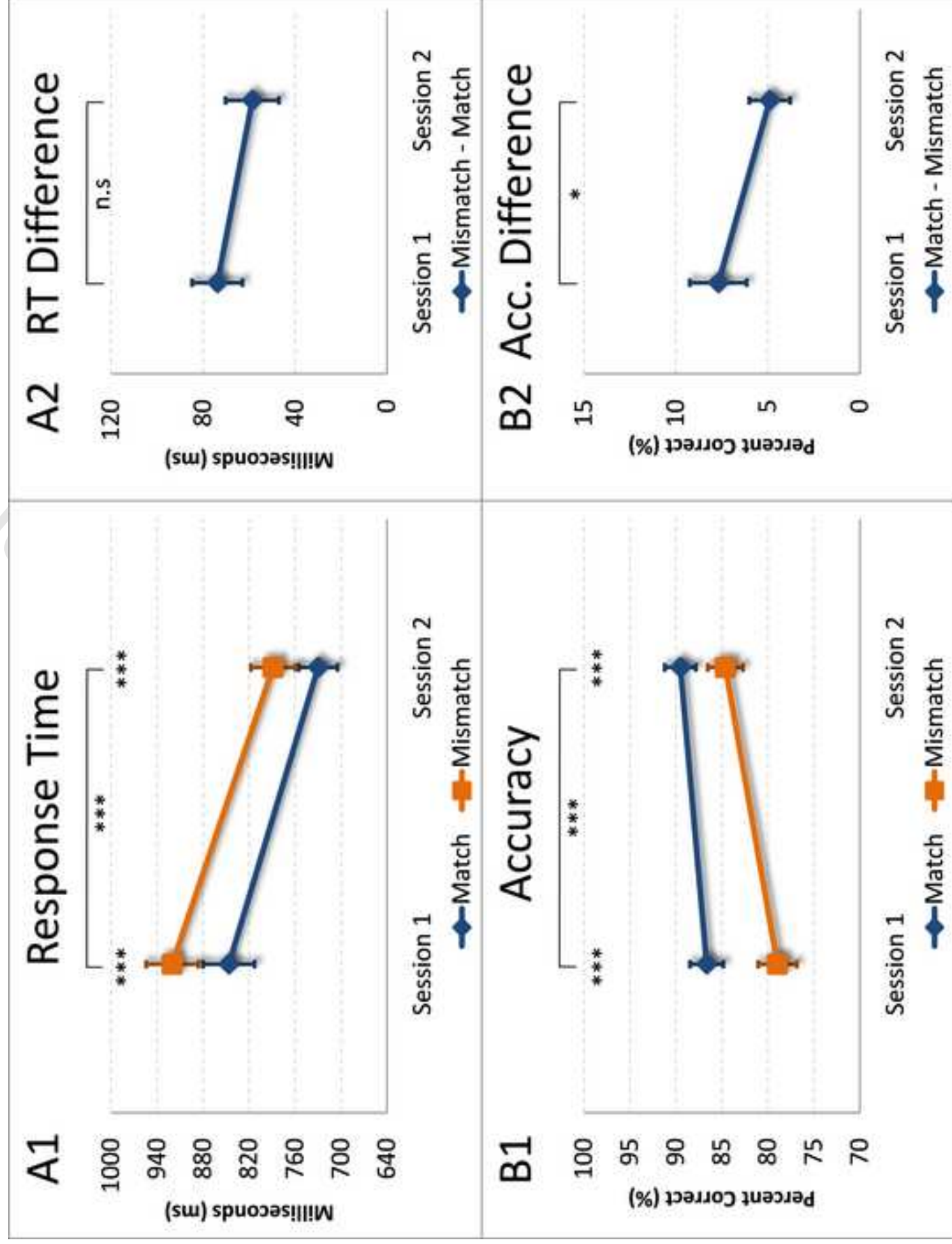


Figure(1)

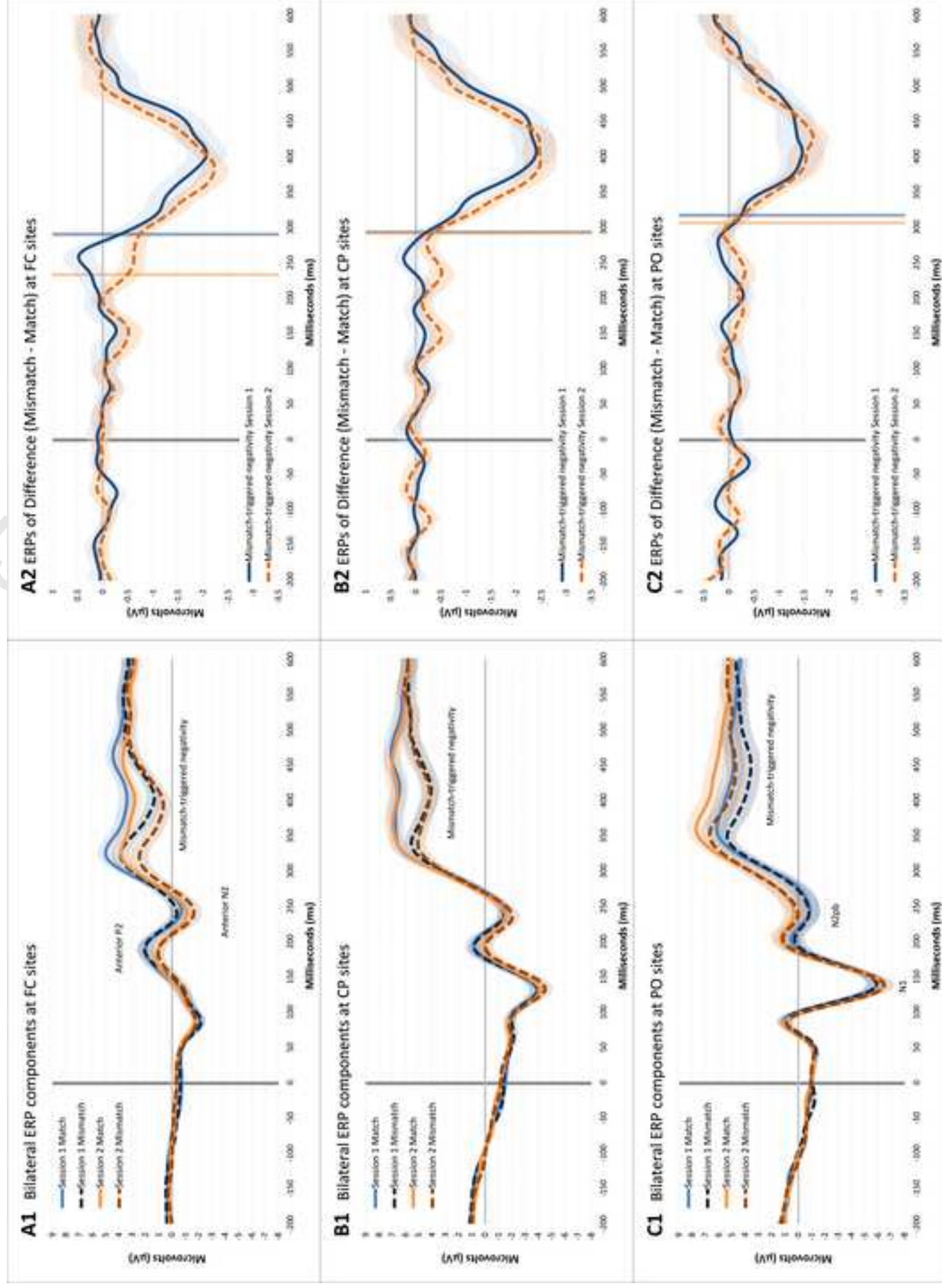
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Figure(2)
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Figure(3)
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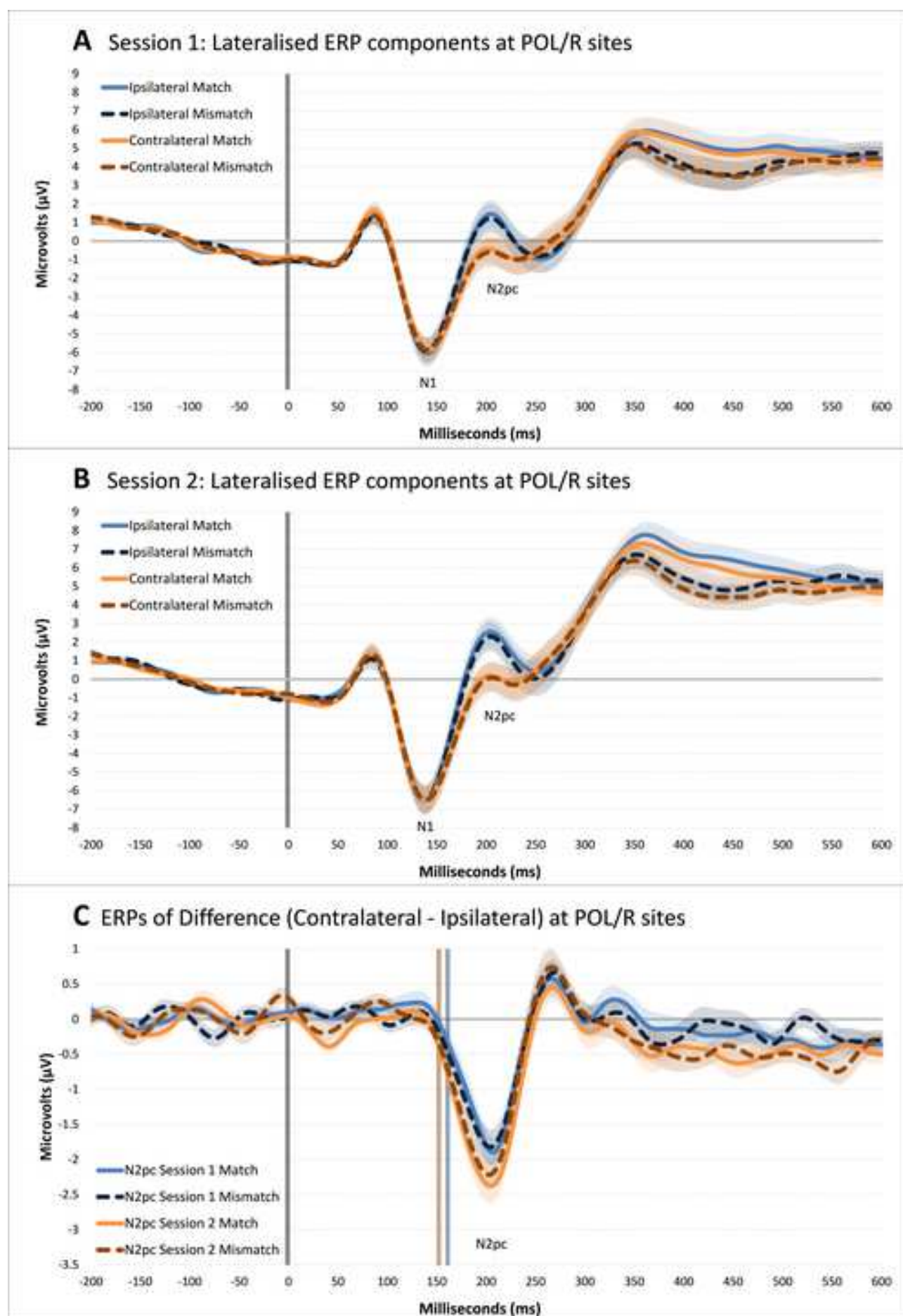


Table 1. Summary of the main effect of practice on latency and amplitude of ERP components (N=27).

	Latency (ms), <i>p</i>	Amplitude (μV), <i>p</i>
N1 at PO ROI	Reduction (~3), *	ns
Anterior P2 at FC ROI	Reduction (~7), *	ns
N2pc at PO ROI	Reduction (~9), (*)	More negative (.48), ***
Anterior N2 at FC ROI	ns	More negative (mismatch) (1.18), *
N2pb at PO ROI	ns	Less negative (1.15), **
MTN at FC ROI	Reduction (~57), **	More negative (.76), *
MTN at CP ROI	ns	ns
MTN at PO ROI	ns	Less negative (1.30), **

Region of Interest (ROI): Fronto-Central (FC); Centro-Parietal (CP); Parieto-Occipital (PO); Mismatch-triggered negativity (MTN); non-significant (ns); (*) $p < .05$ (1-tailed); * $p < .05$ (2-tailed); ** $p < .01$ (2-tailed); *** $p < .001$ (2-tailed).

Table 2. Loadings on each of the three principal components retained from the PCA on average of ERP amplitudes collapsed across sessions, as determined by thresholds from the parallel analyses, shown after Promax rotation. Large loadings have been highlighted in bold to emphasize the variables that contribute to each principal component. Communalities have been also reported (N = 27).

	Components			Communalities
	1	2	3	
Mismatch-triggered negativity at PO ROI	.94	-.05	-.05	.85
N2pb at PO ROI	.78	-.24	.31	.72
Mismatch-triggered negativity at CP ROI	.73	.49	-.16	.87
Anterior N2 at FC ROI	-.28	.91	.17	.88
Mismatch-triggered negativity at FC ROI	.28	.77	-.11	.72
Anterior P2 at FC ROI	-.08	.75	.15	.61
Contralateral N1 at PO ROI	.18	.04	.92	.95
Ipsilateral N1 at PO ROI	.17	.05	.91	.93
N2pc at PO ROI	-.33	.13	.59	.43

Table 3. Pearson's product-moment correlations and modified Pearson-Filon (ZPF) test results comparing correlation coefficients between two variables at two different time points (N = 27).

	Session 1 correlation coefficient, <i>p</i>	Session 2 correlation coefficient, <i>p</i>	ZPF score, <i>p</i>
A) Mean accuracy with mean amplitude of N2pc at PO ROI for mismatch trials	.17, ns	-.21, ns	1.98, *
B) Mean RTs with mean peak latency of bilateral N2pb at PO ROI for match trials	-.19, ns	.19, ns	-2.40, *
C) Mean RTs with mean peak amplitude of bilateral N2pb at PO ROI for match trials	-.06, ns	.29, ns	-2.15, *
D) Mean RTs with mean peak amplitude of bilateral N2pb at PO ROI for mismatch trials	-.12, ns	.21, ns	-2.21, *
E) Mean RTs for match trials with mean onset latency of MTN at FC ROI	-.52, **	.23, ns	-2.54, *
F) Mean RTs for mismatch trials with mean onset latency of MTN at FC ROI	-.48, *	.36, ns	-2.83, **
G) Mean RTs with mean amplitude of MTN at FC ROI for mismatch trials	-.18, ns	.29, ns	-2.57, **
H) Mean RTs with mean amplitude of MTN at CP ROI for mismatch trials	-.28, ns	.24, ns	-3.24, **
I) Mean RTs with mean amplitude of MTN at PO ROI for mismatch trials	-.30, ns	.01, ns	-2.02, *
J) Mean onset latency N2pc with mean onset latency of MTN at FC ROI	-.32, ns	.28, ns	-1.99, *
K) Mean onset latency of MTN at FC ROI with mean onset latency of MTN at CP ROI	.85, ***	-.03	4.57, ***
L) Mean peak latency of N2pc at PO ROI with peak latency of N1 at PO ROI for match trials	-.00, ns	.39, *	-1.99, *

Reaction Times (RTs); Region of Interest (ROI); Fronto-Central (FC); Centro-Parietal (CP); Parieto-Occipital (PO); Mismatch-triggered negativity (MTN); non-significant (ns); * $p < .05$ (2-tailed); ** $p < .01$ (2-tailed); *** $p < .001$ (2-tailed). Significances in correlation coefficients are indicated in bold.